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GRAZING AND PREDATION AS RELATED TO ENERGY NEEDS OF STAGE I ZOEAE OF THE TANNER CRAB *CHIONOECETES BAIRDI* (BRACHYURA, MAJIDAE)*

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Abstract

The ability of first-feeding stage I zoea larvae of *Chionoecetes bairdi* to obtain energy from phytoplankton was investigated using a range of phytoplankton cell sizes and cell densities. An early first stage zoea requires approximately 6.8×10^{-3} calories or 0.60 μg carbon (approximately 4% body C) per day for metabolic needs at 5°C. Experiments with dinoflagellates and large centric diatoms demonstrated that the larvae are capable of capturing and ingesting these cells. However, the zoeae grazed at rates which satisfied less than 15% of basal metabolic energy requirements at cell concentrations similar to those prevailing in coastal and shelf sea environments where the crabs are found. Grazing on smaller cells, including chain-forming species common in nature, was not detected. In the laboratory, first-feeding zoeae were capable of consuming zooplankton prey at rates which provided up to 308% of basal metabolic requirements.

Introduction

Laboratory studies have demonstrated that availability and nutritional adequacy of food are among the most important factors affecting survival of crab larvae (Roberts, 1974; Sulkin, 1975, 1978; Sulkin and Epifanio, 1975; Christiansen and Yang, 1976; Sulkin and Norman, 1976; Anger and Nair, 1979). Generally, laboratory diets consisting primarily of zooplankton have provided the highest survival rates (Brick, 1974; Roberts, 1974; Sulkin, 1975, 1978; Bigford, 1978). There is a high degree of morphological similarity of the feeding appendages of crab larvae and numerous reports of their attacking single zooplankton prey (Sato and Tanaka, 1949; Knudsen, 1960; Herrnkind, 1968; Gonor and Gonor, 1973). This evidence has led to the widely held belief that phytoplankton is of limited dietary importance. However, there is evidence that phytoplankton may be a common component of the diet of some larvae in nature (*e.g.,* LeBour, 1922, 1927). Laboratory studies with the larvae of a brachyuran crab (Hartman and Letterman, 1978) and a pandalid shrimp (Stickney and Perkins, 1981) indicated that phytoplankton diets can significantly prolong the life of these larvae compared to unfed control animals, even though both larvae showed markedly better survival on zooplankton diets. Both studies noted that specimens collected at sea contained phytoplankton in the stomachs. Roberts (1974) and Sulkin (1975) reported that the larvae of crabs used in their experiments (an anomuran and brachyuran crab, respectively) consumed phy-

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toplankton in laboratory studies and that this prolonged survival slightly compared to unfed zoeae. In contrast, Atkins (1955) and Bousquette (1980) were able to rear the larvae of pinnotherid (brachyuran) crabs through all zoeal stages to the megalops stage with phytoplankton alone, but the authors did not specify survival times of unfed controls. Despite the large body of evidence that zooplankton are the primary prey for larvae of most species of crab, it appears that a functional role for phytoplankton cannot be ruled out for all species.

In the genus *Chionoecetes,* both zoeal stages of *C. opilio* have been successfully cultured when fed the nauplii of *Artemia* sp. alone (Motoh, 1973) and combined with rotifers, *Brachionus plicatilis* (Kon, 1970, 1979). Using natural prey, Paul *et al.* (1979) reported that stage I zoeae of *C. bairdi* can consistently capture copepods, copepodids, and copepod nauplii when these prey are offered at densities of 20–40 per liter. However, the requirement of prey concentrations above 20 per liter for consistent prey capture suggested that there may be times when zooplankton prey are not present in sufficient numbers to ensure successful feeding by the zoeae.

An alternate, or supplementary, food source might be phytoplankton, which are more abundant than zooplankton and are perhaps more easily captured. Bright (1967) reported that the principal stomach contents of Tanner crab zoeae collected from Cook Inlet, Alaska, were unidentified diatoms; little zooplankton material was reported. In the southeastern Bering Sea, thecate dinoflagellates were found along with parts of copepods, pteropods, tintinnids, and other zooplankters in the stomachs of stage I and stage II zoeae of *Chionoecetes* spp. (K. O. Coyle, Univ. of Alaska, pers. comm.). Examining specimens from the same region in later years. Incze and Armstrong (unpubl. observations) found little evidence of zooplankton in the stomachs of stage I and stage II zoeae, but frequently found solitary and chain-forming centric diatoms. Although these observations suggest that phytoplankton may be an important component in the diet of these zoeae, the relative value of this material to these larvae is unknown.

Currently, there exists little information on relationships between type and availability of prey and feeding success of crab zoeae in the ocean. Consequently, we know little about this major determinant of larval survival. The objective of this study is to evaluate the relative value of phytoplankton in supplying the energy (calories) or material (carbon) needed for maintenance metabolism and growth of the first feeding stage I zoeae of *C. bairdi* (for a description of this stage, refer to Haynes, 1973). First-feeding zoeae were used because they (1) are unaffected by previous feeding experience and (2) co-occur with the spring phytoplankton bloom which precedes development of the zooplankton community in Alaskan waters.

Materials and Methods

Several egg-bearing female crabs captured near Kodiak, Alaska, were held in circulating sea water tanks at 4–5°C. Zoeae hatched continually and tanks were drained each day before an experiment so that only freshly hatched, actively swimming zoeae were used. All respiration and feeding experiments were conducted at 5°C. Stage I zoeae normally encounter temperatures of 4 to 6°C in Alaskan waters.

Respiration rates of 12-hour old stage I zoeae were measured in a glass differential syringe manometer (Umbreit *et al.,* 1972). The 15 ml respirometer vessel held 4 to 6 unfed zoeae, 6.0 ml of 1.0 μm filtered sea water, and 0.1 ml 20% KOH to absorb CO_2. The active zoeae were acclimated to vessel temperature for one hour before the manometers were sealed. Observations of oxygen uptake were made after a minimum of five hours. Shaking of the respirometers was restricted to the last 10 minutes of the final observation. There were eight replications for respiration rate

(VO_2) measurement. Oven dried weights (60°C) of the zoeae from each observation of VO_2 were determined with an electrobalance. Values of VO_2 were converted to calories using the conversion 4.73×10^{-3} cal · μl 0_2^{-1} (Brody, 1945). Carbon equivalents of VO_2 were calculated using a respiratory quotient (RQ) of 0.90 for phytoplankton prey and 0.75 for zooplankton prey and unfed zoeae. Values of RQ (Giese, 1973) were assigned based on the approximate proportion of carbohydrate, lipid and protein in phytoplankton (Parsons *et al.*, 1961) compared to zooplankton (Corner and Cowey, 1968) and *Chionoecetes* spp. zoeae (Incze, 1983). Adjusting RQ values to account for the possible range of substrate proportions in phytoplankton and in zooplankton produces minor changes in the estimated carbon equivalents of VO_2.

Ingestion rates of one day old zoeae were measured using animal and plant prey in several ways. Rates of ingestion of newly hatched *Artemia* sp. nauplii (San Francisco Bay variety) by one day old zoeae were determined by placing 50 nauplii in 500 ml of 1 μm filtered sea water in a lightly aerated 550 ml black plastic beaker containing five zoeae. The zoeae were allowed to feed for 24 hours in a 12 hour light, 300 lux:12 hour dark cycle at 5°C. Three hundred lux was approximately 2% of light intensity at sea surface during the experiments. Nauplii remaining after 24 hours were counted under a microscope. Forty replicate prey consumption measurements were made. A caloric value of 8.7×10^{-3} cal (calculated from data of Levine and Sulkin, 1979) and a carbon value of 1.2 μg C (present study) per nauplius were used to estimate the value of the ingested ration. Carbon was measured on a Perkin-Elmer Model 240 elemental analyzer. Six beakers containing only nauplii were used to demonstrate that all prey were recovered during subsequent recounts. An assimilation efficiency of 0.70 (Conover, 1966) was assumed.

Rates of ingestion of various phytoplankton cells by one day old zoeae were investigated by (1) comparing chlorophyll concentrations in initial, grazed, and control containers using cultured algae, and (2) counting cells in initial, grazed, and control containers for selected algal species. Phytoplankton cells representative of the shape and size of those found in the planktonic environment and stomachs of *C. bairdi* zoeae were used. Mono-specific cultures of *Phaeodactylum tricornutum, Chaetoceros compressus, Gonyaulax grindleyi (Prorocentrum reticulatum),* and an unidentified thecate dinoflagellate (referred to here as F16) were among the algae used. Grazing experiments were also conducted with large centric diatoms (*Coscinodiscus* spp. and *Thalassiosira* spp.) removed from plankton samples collected with a vertical tow using a 44 μm mesh net. All experiments were conducted at 5°C in a 12 hour light, 300 lux:12 hour dark cycle. Experimental containers were placed on a slowly rotating wheel. The size and shape of phytoplankton cells used in these experiments are provided in Table I.

Different container sizes were used for cultured versus sorted, natural phytoplankton. Grazing experiments and controls using the cultured algae were conducted in 250 ml translucent polyethylene bottles. Approximately 100 zoeae were placed in each bottle; accurate counts of zoeae were made at the end of each experiment. Four algal food concentrations corresponding to chlorophyll concentrations of approximately 2, 10, 50, and 100 μg chl a per liter were used. Replicates of all experimental conditions were run. Gut flourescence of zoeae and chlorophyll concentrations of initial, grazed and control media were measured using a Turner Model 111 fluorometer, media sample volumes up to 200 ml, and extraction volumes of 10 ml (Strickland and Parsons, 1968).

From a separate series of cell count experiments with *G. grindleyi* cultures, cell count samples (40–60 ml) were preserved from initial, experimental and control vessels with 0.2 ml Lugol's solution. Cells were counted using a settling chamber

TABLE I

Approximate size and shape of phytoplankton cells used in grazing experiments with the first zoeae of Chionoecetes bairdi

Phaeodactylum tricornutum	pennate, 7 × 21 μm
Chaetoceros compressus	individual centric cells, 10 μm diameter; average chain length, 8–11 cells, 90–120 μm; average chain width (with spines), 90 μm.
dinoflagellate F16	10 × 15 μm
Gonyaulax grindleyi	35–45 μm, roughly symmetrical but irregularly shaped
Conscinodiscus spp.	centric, 71 μm (height) × 222 μm (diameter)
Thalassiosira spp.	centric, 100 μm (height) × 168 μm (diameter)

and an inverted microscope (Utermohl, 1958). A minimum of 400 cells was counted for each estimate of cell density (Lund *et al.*, 1958) and three to four replicate counts were made of each sample (initial, control, and experimental) at the highest and lowest cell densities. To determine carbon content of phytoplankton cells, samples of culture were collected with a 500 μl Oxford pipette and dispensed in a carefully measured volume of filtered sea water for cell counts and on pre-combusted Gelman Type A/E glass fiber filters for CHN analysis. Carbon content of the cells was measured using a Perkin-Elmer Model 240 elemental analyzer.

Grazing experiments and controls using *Coscinodiscus* and *Thalassiosira* cells removed from natural phytoplankton were conducted in 60 ml transluscent plastic bottles containing five zoeae each. Cells were individually counted before and after a 24 hour feeding period. Cell carbon content was estimated from cell volume according to the method of Strathmann (1967).

Average cell concentrations during each experiment were calculated according to the method prescribed by Frost (1972) which assumes that the number of cells during an experiment changes at a constant exponential rate. The equation corrects for the growth of phytoplankton measured in control containers. All relationships between ingestion and cell concentration were calculated using the average cell concentration value. The functional response of zoeae grazing on dinoflagellates at various cell densities was plotted using the Holling "disc" equation (Holling, 1959) which treats each capture of a food particle as an independent event.

Carnivorous feeding activity of zoeae on *Artemia* sp. nauplii was compared in the presence and absence of a natural spring bloom phytoplankton assemblage collected in Resurrection Bay, Alaska. A 10 liter Niskin bottle, cast at approximately 1 m depth, was used to collect the phytoplankton. A sample from the bottle was concentrated by pouring the sea water through a 40 μm mesh sieve resting in an over-flow vessel. All conspicuous zooplankton and most conspicuous micro-zooplankton were removed from this sample under a microscope. The remaining phytoplankton was diluted with filtered sea water to return the sample to its original volume for use in feeding observations. Two subsamples were examined to obtain the initial phytoplankton concentration (Lund *et al.*, 1958). Large solitary cells and long chain-forming species were retained at approximately their original concentrations by the procedure; these are the cell types seen in the stomachs of zoeae from plankton collections. The assemblage contained *Chaetoceros* spp. chains at approximately 5.5×10^4 cells l^{-1} and large centric diatoms at approximately 1.2×10^1 l^{-1}. Four groups of five zoeae each were placed in 250 ml vessels containing the following

prey assemblages: 60 nauplii l^{-1}, 96 nauplii l^{-1}, 60 nauplii l^{-1} and bay phytoplankton, and 96 nauplii l^{-1} and bay phytoplankton. There were 10 replicates for each prey assemblage. At the end of the experiments, surviving nauplii were counted and zoea stomachs were examined under a microscope for phytoplankton cells.

Results

Oxygen consumption rates (VO_2) of one day old stage I *C. bairdi* zoeae averaged 1.3 μl $O_2 \cdot$ mg dry wt^{-1} h^{-1} at 5°C (Table II). The average dry weight of an individual zoea within 24 hours of hatching was 47.8 ± 7.6 μg, so the corresponding value of VO_2 was 0.06 μl O_2 $zoea^{-1}$ h^{-1}. The energy required for respiratory metabolism (R) of first feeding zoeae at this temperature was estimated to be 6.8×10^{-3} cal $zoea^{-1}$ d^{-1}. Carbon equivalents of respiration were 0.59 and 0.71 μg C $zoea^{-1}$ d^{-1} using respiratory quotients (RQ) of 0.75 and 0.90, respectively. Stage I zoeae were approximately 33% C (based on dry weight); therefore, respiratory energy needs ranged from 3.7 to 4.5% body C $zoea^{-1}$ d^{-1}.

The average daily feeding rate of one day old zoeae was one *Artemia* nauplius per zoea (range: 0.2 to 2.2) at 5°C when prey were offered at initial densities of 100 per liter (Table II). The average assimilated carbon values of prey consumed in individual experiments ranged from 28 to 308 percent of the mean respiratory energy needs of each zoea.

The Student *t*-test comparing predation rates in the presence and absence of phytoplankton showed no significant differences ($P < 0.05$) in the number of nauplii consumed in the two groups. At 60 prey per liter, the average daily consumption rates per zoea were 1.0 ± 0.5 and 0.9 ± 0.4 nauplii in the presence and absence of phytoplankton, respectively. Corresponding values at 96 prey per liter were 1.4 ± 0.5 and 1.0 ± 0.2 nauplii $zoea^{-1}$ d^{-1}. No phytoplankton cells were found in the stomachs of the zoeae at the end of the experiment.

Chlorophyll a measurements (μg $liter^{-1}$) of replicate initial, control and experimental grazing bottles showed no detectable difference for *P. tricornutum, C. compressus,* or F16 experiments at any of the chlorophyll concentrations employed. Likewise, no discernible difference in gut flourescence between fed and unfed zoeae was found in any of the above experiments. A slight decrease was found in some of the grazed bottles of *G. grindleyi* cells, and some measurements of gut flourescence of zoeae from these experiments showed higher levels in fed than unfed animals. However, all measurements were at the limits of sensitivity of the methods and, when the experiments were repeated, results were not consistent between trials or between replicates.

Data from the cell count experiments with *G. grindleyi, Coscinodiscus* spp. and *Thalassiosira* spp. are summarized in Table III, along with a comparison of ingested ration (carbon) and respiratory requirements of the zoeae. No phytoplankton growth was observed in control vessels. Over the range of cell concentrations used, zoeae obtained an average of 1.4 to 14% of their respiratory energy requirements from phytoplankton. The relationship between ingestion (grazing) rate of zoeae and average cell concentration is shown in Figure 1 for dinoflagellates and Figure 2 for large centric diatoms. The functional response of zoeal ingestion rate to increases in dinoflagellate abundance demonstrated a leveling at cell concentrations above 8.0×10^4 l^{-1} (Fig. 1).

The coefficient of variation of replicate cell counts of samples from the *G. grindleyi* experiments was less than 9% at the lowest cell densities used and less than 5% at the highest. No subsampling variability was associated with the *Coscinodiscus*

TABLE II

Oxygen consumption (VO_2), respiratory requirement (R) and ingested ration (I) of 24 hour old zoeae preying on nauplii of Artemia *sp. at 5°C. Percent contribution of ingested ration to metabolic requirement (%R) is estimated*

	VO_2			R(zoea^{-1} d^{-1})		I(zoea^{-1} d^{-1})			%R[1]	
	$\mu l \cdot mg$ dry wt^{-1} h^{-1}	$\mu l \cdot$ zoea^{-1} h^{-1}	Dry wt. (μg zoea^{-1})	cal $\times 10^{-3}$	μg C	No. nauplii	cal $\times 10^{-3}$	μg C	cal	C
$\bar{X}$	1.3	0.06	47.8	6.8	0.60	1.0	8.7	1.2	89	140
sd	0.3	0.01	7.6	1.1	0.13	0.9	7.8	1.1	80	128
Range	1.06–1.89	0.05–0.07	38.0–56.0	5.7–7.9	.48–.87	0.2–2.2	1.7–19.0	0.24–2.64	18–196	28–308

[1] Calculation is based on the mean respiratory requirement and assumes an assimilation efficiency of 0.70.

TABLE III

*Ingestion rate (I) of 24 hour old zoeae grazing on phytoplankton (*Gonyaulax grindleyi, Coscinodiscus *spp.,* Thalassiosira *spp.) at various cell concentrations (⟨C⟩) at 5°C, and percent contribution to respiratory requirement (%R)*

Cell type	Carbon (μg cell^{-1})	⟨C⟩ (cells l^{-1})	I (zoea^{-1} d^{-1}) No. cells	I (zoea^{-1} d^{-1}) μg C	%R[1]
G. grindleyi	2.9×10^{-3}	7.3×10^{3}	4.3	1.2×10^{-2}	1.4
		3.1×10^{4}	19.0	5.0×10^{-2}	5.8
		6.5×10^{4}	33.6	9.7×10^{-2}	11.3
		1.2×10^{5}	39.9	1.2×10^{-1}	14.0
Coscinodiscus spp.	2.66×10	7.8×10^{2}	2.6	6.8×10^{-2}	7.9
		8.40×10^{2}	2.9	7.6×10^{-2}	8.9
		8.80×10^{2}	2.7	7.0×10^{-2}	8.2
		9.40×10^{2}	2.4	6.3×10^{-2}	7.4
		9.83×10^{2}	2.3	6.0×10^{-2}	7.0
		9.83×10^{2}	2.3	6.0×10^{-2}	7.0
		1.68×10^{3}	2.2	5.7×10^{-2}	6.6
		1.68×10^{3}	2.5	6.6×10^{-2}	7.7
		1.68×10^{3}	4.2	1.1×10^{-1}	12.8
Thalassiosira spp.	2.30×10	6.26×10^{2}	1.5	3.6×10^{-2}	4.2
		1.66×10^{3}	2.7	6.4×10^{-2}	7.5

[1] Calculation is based on a mean respiratory requirement of 0.6 μg C zoea^{-1} d^{-1} (from Table II), an RQ of 0.9 and an assimilation efficiency of 0.70.

or *Thalassiosira* experiments since all cells were individually added to, and removed from, the experimental and control vessels and counts were double-checked.

DISCUSSION

Respiration rates measured at 5°C in this study are lower than those reported for many decapod larvae that inhabit warmer environments (see Mootz and Epifanio, 1974; Schatzlein and Costlow, 1978; Levine and Sulkin, 1979). However, the hourly weight-specific rates for stage I *C. bairdi* zoeae ($\bar{X}$ = 1.3 μl O_2 · mg dry wt^{-1} · h^{-1}) are similar to those of first stage zoeae of *Cancer borealis* (1.3 μl O_2) and *C.*

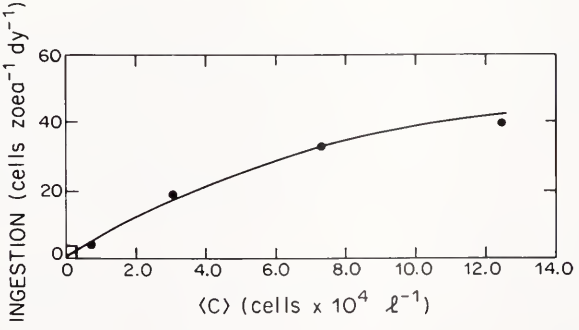

FIGURE 1. Relationship between ingestion (I) and average cell concentration (⟨C⟩) of *G. Grindleyi*. The curve was fit using the Holling equation (Holling, 1959). Area of I/⟨C⟩ observations for large centric diatoms (Fig. 2) shown by box in lower left corner.

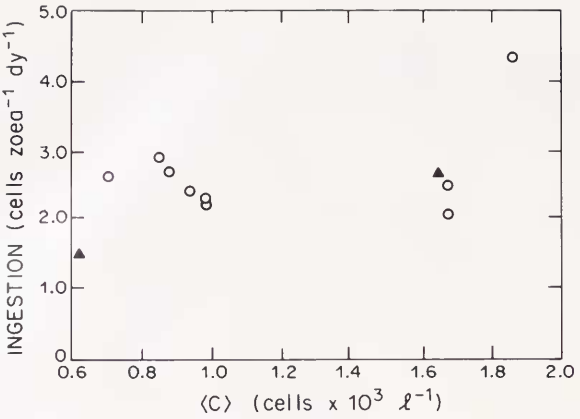

FIGURE 2. Relationship between ingestion (I) and average cell concentration (⟨C⟩) of large centric diatoms: *Coscinodiscus* spp. (○); *Thalassiosira* spp. (▲).

irroratus (1.7 μl O_2) measured at 5°C by Sastry and McCarthy (1973). Furthermore, the respiration rates measured in this study are corroborated by estimated *in situ* stage I growth rates and by VO_2 measurements of stage II zoeae captured at sea. The estimated growth rates of *C. bairdi* first stage zoeae from the southeastern Bering Sea (3.9 to 4.7% body C zoea^{-1} d^{-1}: Incze, 1983) are almost identical to the carbon equivalents of respiration measured in this study (3.7 to 4.5% body C zoea^{-1} d^{-1}). This agrees with the findings of laboratory studies of other crab species where zoeal respiration and growth of early stages were approximately equal (Mootz and Epifanio, 1974; Levine and Sulkin, 1979). In another study (Incze, 1983), measurements of VO_2 of 550 to 590 μg dry weight stage II *C. bairdi* zoeae captured with a plankton net were obtained with a Radiometer blood-gas analyzer following methods of Laughlin *et al.* (1979) and using incubation volumes of 10 and 20 ml. The allometric equation relating respiration (R) to dry body weight using the results of the stage I and stage II measurements provides a weight exponent of 0.72 ($R = 1.198\ W^{0.72}$: Incze, 1983), a value similar to those reported for other decapod larvae (Schatzlein and Costlow, 1978) and for animals in general (McMahon, 1973). Estimated *in situ* growth rates of stage I zoeae and respiration rates of stage II zoeae therefore substantiate the results obtained from the small-volume manometric methods used on first stage larvae in this study.

The ability to feed on a wide variety of prey particles is one adaptation for procuring food in a diverse and dispersed community. Many planktonic organisms employ this strategy of omnivorous feeding, though they may do so to different degrees (Marshall, 1973; Landry, 1981). Despite its advantages, omnivory may involve compromises in structure and function of feeding appendages which decrease feeding performance on certain types of prey. For instance, Robertson and Frost (1977) found that *Aetidius divergens* could feed efficiently on large diatoms and *Artemia* nauplii, but was inefficient at ingesting small diatoms when compared with herbivorous calanoid copepods.

Measurements made in this study demonstrate that *C. bairdi* zoeae are omnivorous and consume some phytoplankton. Since large phytoplankton cells were captured and ingested in the absence of zooplankton prey, directed grazing activity is indicated. However, in these experiments, grazing rates were too low to meet respiratory energy requirements, even assuming that variations in individual zoeal

grazing rates existed. The functional response (Fig. 1) of zoeae grazing on dinoflagellates indicates that ingestion rates would not increase substantially at cell concentrations higher than 2×10^5, presumably because feeding ability is saturated. Consequently, cells of this size could not sustain the zoeae. Even the large diatoms, which contained about ten times as much carbon per cell as the dinoflagellates, could not sustain zoeae under most natural conditions. It would require approximately 2×10^5 of these large cells per liter to satisfy the respiratory requirements of *C. bairdi* first-feeding zoeae, assuming the same functional feeding response to large diatoms and dinoflagellates at high cell concentrations. However, this would be an extraordinarily high concentration for diatoms of this size in the upper 20 m of the ocean where most of the larvae are found (Incze, 1983). When growth requirements averaging about 4.3% body C zoea^{-1} d^{-1} (see above) are added to respiratory requirements, the contribution of phytoplankton to total energy needs is further diminished. However, a nutritional role for phytoplankton, such as providing micro-nutrients, is not ruled out by these findings.

The chlorophyll method employed with the grazing experiments which used cultured algae was useful as a screening process to see if measurable chlorophyll depletion (cell consumption) occurred with any of the cells used. The technique verified that there were no instances where rates of consumption satisfied basal metabolic needs, since these rates would have been detected. However, the method was clearly not sensitive enough to measure the low grazing rates observed in cell count experiments using *G. grindleyi*.

The measurements of carnivorous feeding rates in the presence and absence of a natural phytoplankton assemblage collected at the time that *C. bairdi* zoeae were hatching in Resurrection Bay indicated that zoeal predation was unaffected by the phytoplankton. Since none of the conspicuous chain-forming diatoms from the assemblage were found in the stomachs of the zoeae at the end of the experiments, it appears that little or no grazing occurred. However, it is not known whether the apparent lack of grazing in these experiments reflects specific predatory behavior directed at the larger zooplankton or simply a high probability of predator-nauplius encounter at the prey densities used. It may be that diatoms and dinoflagellates appear frequently in the stomachs of zoeae collected from the plankton because more time is spent grazing when zooplankton prey are less available than in these experiments. When phytoplankton cells are consumed, they may only appear quantitatively important because their thecae are conspicuous and may not be digested rapidly. Softbodied prey, such as nauplii, have few hard parts which can be identified in zoea stomachs, and the hard parts of other zooplankters may be rejected during feeding (Fowler *et al.*, 1971; Mauchline, 1980). Their stomachs could also contain phytoplankton if zoeae proved to be coprophagous feeders (see data on fecal pellet sizes and contents presented by Urrère and Knauer, 1981). Additional laboratory observations on the ability of zoeae to consume specific species and developmental stages of zooplankton, as well as fecal pellets, are necessary to complement the stomach analysis of individuals feeding *in situ*.

In the zooplankton prey consumption rate experiments, it is likely that some non-feeding zoeae were included, since only individuals no more than 24 hours old and with no previous feeding experience were used. Work by Kon (1979) suggests that a three day "critical" period exists during which first stage zoeae must initiate feeding before subsequent mortality increases markedly. Thus it is probable that newly molted stage I zoeae of this genus have some stored energy that can be used to meet metabolic energy requirements. The occurrence of some non-feeding individuals in experiments may explain why, on the average, only enough energy was

obtained to meet metabolic requirements. We stress, however, that there were some groups of zoeae which consumed zooplankton prey at rates which provided over 300% of daily carbon needs. It is reasonable to assume that similar differences occur during predation on natural prey. The relative abundance of first-feeding larvae which are competent predators under various planktonic conditions may be an important aspect of year-class survival.

Although appropriate zooplankton prey must be rare compared with phytoplankton, they are probably a major component of the zoeal diet of *C. bairdi*. Zoeae of this species do not appear to be well adapted to handling a large number of small prey. These experiments used only 24 hour old first-feeding zoeae, but the larvae demonstrated competence at feeding by capturing and ingesting *Artemia* nauplii (present study) and active zooplankton prey (Paul *et al.*, 1979). Larval growth should increase the relative disadvantage of the predator-prey size relationship with respect to phytoplankton. Unless behavioral or morphological changes occur which favor grazing, phytoplankton should remain a comparatively minor source of energy in larval development of this species.

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